Systematic Entomology (2003) **28**, 23–37

Phylogenetic reassessment of the five forewing radial-veined tribes of Riodininae (Lepidoptera: Riodinidae)

JASON P. W. HALL

Department of Systematic Biology-Entomology, National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A.

Abstract. The relationships among the genera and tribal groupings of Riodininae with five forewing radial veins, and between these and tribes with four forewing radial veins, were examined using a phylogenetic analysis. Using the type species from all sixteen genera in the tribal groupings Eurybiini, Mesosemiini and *incertae sedis* (a presumed paraphyletic group of loosely related genera), and representatives from the four forewing radial-veined riodinine tribes, thirty-five new and traditional characters were coded from adult ecology, wing venation and pattern, the adult head and body, male and female genitalia, and early stage ecology and morphology. The majority of characters are illustrated. Phylogenetic analysis of these data produced five equally most parsimonious cladograms using equal weights and after successive weighting. The strict consensus of these confirms the monophyly of Eurybiini and Mesosemiini as currently conceived, but also indicates several higher-level relationships not previously hypothesized. Mesosemiini is here more broadly defined to also include the entire *incertae sedis* section, and the tribe is divided into Mesosemiina, for the previously delimited Mesosemiini plus *Eunogyra* and *Teratophthalma*, and Napaeina, subtr.n. for the *incertae sedis* section minus these two genera. The following hypothesis of relationships is tentatively proposed for the basal clades of Riodininae: Mesosemiini + (Eurybiini + remainder of Riodininae). These new hypotheses, and the characters supporting them, are discussed and compared with those previously proposed.

Introduction

Despite being conspicuous for its great morphological and ecological diversity, Riodinidae has historically been understudied at the expense of the larger and more showy families of butterflies. The illustrious Henry Walter Bates (1868) was the first author to consider the higher classification of Riodinidae, and he created three subfamilies and several further divisions based on a limited number of characters of wing venation, antennae and palpi. By the early part of the twentieth century, a more accurate picture of the true diversity of the family had emerged, and Stichel (1910–1911, 1928, 1930–1931) was able to produce the first widely accepted classification, using a considerably broader range of morphological characters. He recognized two subfamilies and many tribal and subtribal divisions. The most recent higher classification of the family, and the first to explicitly attempt to recognize only monophyletic groups, was that of Harvey (1987). Based on the most extensive examination of internal and external adult and early stage morphological characters to date, he recognized five subfamilies, the Old World Nemeobiinae (= Hameariinae auctt.) and the considerably more species-rich New World Euselasiinae, Styginae, Corrachiinae and Riodininae, with eleven tribes for Riodininae. Subsequently, Styginae and Corrachiinae were preliminarily merged as a single tribe within Euselasiinae by Hall & Harvey (2002), and the number of tribal groupings within Riodininae was reduced to nine by Hall (1998, 1999).

It has long been recognized (Bates, 1868; Stichel, 1910–1911, 1930–1931) that the largest subfamily, Riodininae, could be divided into those genera possessing the plesiomorphic condition of five forewing radial veins (FRV) (now

Correspondence: Jason Hall, Department of Systematic Biology-Entomology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560-0127, U.S.A. E-mail: jpwhall@hotmail.com

in tribes Mesosemiini and Eurybiini, and *incertae sedis* I) and those possessing the apomorphic condition of four FRV (now in tribes Riodinini, Helicopini, Symmachiini, Stalachtini and Nymphidiini, and *incertae sedis* II). Although the latter grouping is believed to be monophyletic (Harvey, 1987), it has been unclear whether the former constituted a clade or a grade. The two *incertae sedis* groups were erected by Harvey (1987) for paraphyletic assemblages of genera that lacked the synapomorphies for his newly defined tribes, and whose phylogenetic affinities were thus uncertain. This paper presents the results of a phylogenetic study to determine how the genera of the five FRV *incertae sedis* section are related to each other and those in the remaining five FRV tribes, and thus how best they should be formally classified, and how all of these genera are related to those with four FRV.

Methods

Taxa studied

The phylogenetic analyses included the type species of all sixteen riodinine genera with five FRV (see Fig. 1), in the tribal groupings Mesosemiini and Eurybiini, and *incertae sedis* (listed in Table 1), and an additional two distantly related genera to represent the four FRV group of tribes. A more exhaustive sampling of the four FRV tribes would have been beyond the goals and scope of this study. However, to better understand the distribution of characters within each of the five FRV genera, in addition to the type species, the internal and external adult morphology of males and females (where known) was examined in all species of *Alesa*, *Mesophthalma*, *Perophthalma* and all nine *incertae sedis* section genera (as part of a species-level revision, Hall & Harvey, unpublished), and about one-quarter of the species in *Eurybia*, *Leucochimona*, *Semomesia* and *Mesosemia*. Comments on the distribution of character states within genera are given where relevant in the list of characters below. As neither of the remaining two subfamilies is known to be more closely related to Riodininae than the other, a species of *Euselasia* Hübner, [1819] was used as the outgroup as it typifies the only other Neotropical subfamily, Euselasiinae.

Morphology

Abdomens and legs were usually first placed in hot 10% potassium hydroxide (KOH) solution for approximately 5 min, and the resulting material was stored in glycerol after examination. A list of genital dissections examined for taxa included in the phylogenetic analyses is given in Table 2. Light microscopy was done using an Olympus SZH

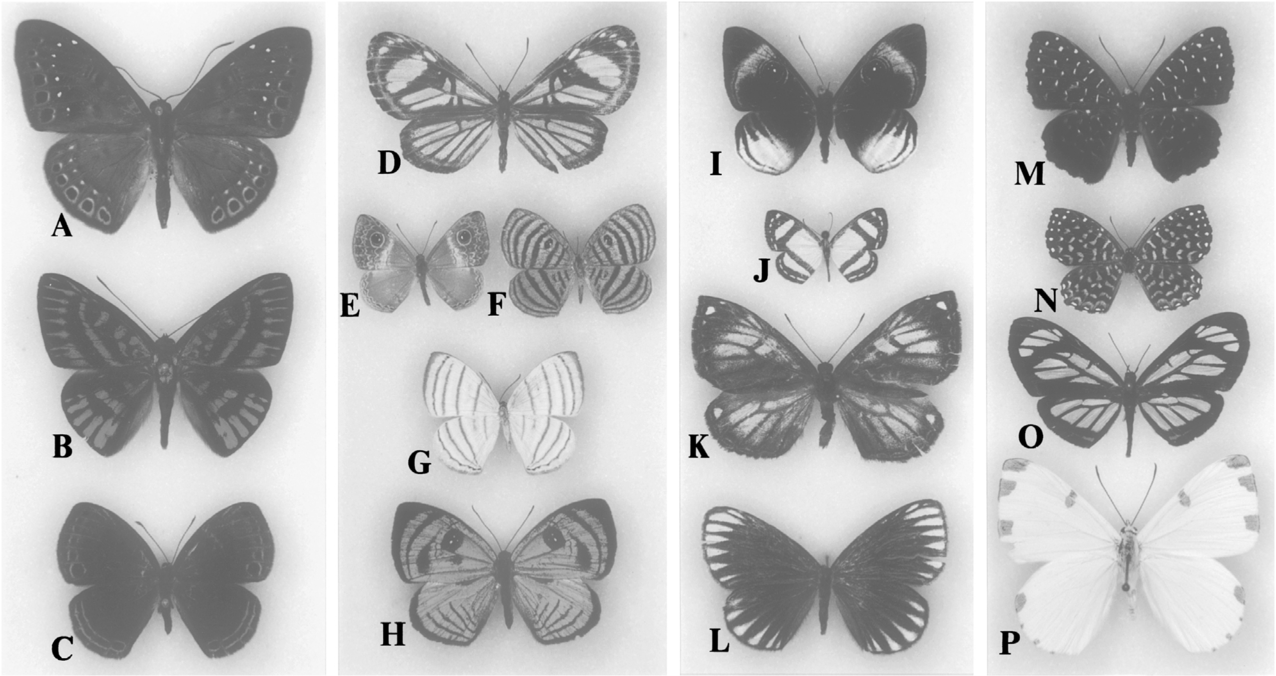

Fig. 1. Type species for all five forewing radial-veined genera in Riodininae. All specimens are males shown on the dorsal surface unless otherwise stated. A, *Eurybia halimede*, Montsinéry, French Guiana; B, *Alesa prema*, Diamantino, Brazil (MGr); C, *Eunogyra satyrus*, Puerto Maldonado, Peru; D, *Teratophthalma phelina* female, Apuya, Ecuador; E, *Perophthalma tullius*, Cerro Pirre, Panama; F, *Mesophthalma idotea*, Iquitos, Peru; G, *Leucochimona icare*, Diamantino, Brazil (MGr); H, *Semomesia croesus*, Saül, French Guiana; I, *Mesosemia philocles*, Vidal, French Guiana; J, *Hyphilaria nicia*, Pimpilala, Ecuador; K, *Eucorna sanarita*, Petrópolis, Brazil (RJ); L, *Voltinia radiata* female, Siquirres, Costa Rica; M, *Napaea eucharila*, Dégrad de Cannes, French Guiana; N, *Cremna actoris*, Puerto Maldonado, Peru; O, *Ithomiola floralis*, Mount Ayanganna, Guyana; P, *Hermathena candidata*, Zamora, Ecuador.

Table 1. Past and present tribal and subtribal classifications for the five forewing radial-veined genera of Riodininae. Genera within higher groupings are listed in the order they appeared in the original works, because that order, at least in Stichel (1910–1911, 1930–1931), was intended to convey information on intergeneric relationships.

Tribal and subtribal arrangements	
Stichel (1910–1911, 1930–1931)	Harvey (1987)
Eurybiini Reuter, 1896	Eurybiini Reuter, 1896
Mesosemiina (as Semomesiina Stichel, 1910)	*Eurybia* [Illiger], 1807
Perophthalma Westwood, [1851]	*Alesa* Doubleday, 1847
Mesophthalma Westwood, [1851]	
Leucochimona Stichel, 1909	Mesosemiini Bates, 1859
Semomesia Westwood, [1851]	*Perophthalma* Westwood, [1851]
	Mesophthalma Westwood, [1851]
Eurybiina	*Leucochimona* Stichel, 1909
Hyphilaria Hübner, [1819]	*Semomesia* Westwood, [1851]
Mesosemia Hübner, [1819]	*Mesosemia* Hübner, [1819]
Eurybia [Illiger], 1807	
Voltinia Stichel, 1910	*incertae sedis* of Harvey (1987)
Hermathena Hewitson, 1874	*Hyphilaria* Hübner, [1819]
Ithomiola C. & R. Felder, 1865	*Voltinia* Stichel, 1910
Teratophthalma Stichel, 1909	*Hermathena* Hewitson, 1874
Alesa Doubleday, 1847	*Ithomiola* C. & R. Felder, 1865
Napaea Hübner, [1819]	*Teratophthalma* Stichel, 1909
Cremna Doubleday, 1847	*Cremna* Doubleday, 1847
Eucorna Strand, 1932 (as *Eucora* Schaus, 1902)	*Napaea* Hübner, [1819]
Eunogyra Westwood, [1851]	*Eunogyra* Westwood, [1851]
	Eucorna Strand, 1932

(magnification up to ×128) and digital images taken using a Nikon HC-300Zi attached to a Wild M400 microscope. Scanning electron microscopy was conducted using a Leica Stereoscan 440 with material mounted on aluminium stubs using carbon tape, and sputter coated with gold/palladium. Adult material that was stored in glycerol was rinsed with 75% ethanol and air-dried before mounting. Larval material was critical-point dried in a Samdri 790 machine before mounting. The terminology for male and female genital and abdominal structures follows Klots (1956) and Eliot (1973), and nomenclature for venation follows Comstock & Needham (1918), with cells named for the vein above.

Cladistic analyses

The phylogenetic analyses, based on maximum parsimony, were performed using heuristic searches with 500 random addition sequence TBR replicates in PAUP version 4.0b4a (Swofford, 1999). All characters were equally weighted and unordered, therefore making no *a priori* assumptions about the relative importance of characters or the evolutionary history of their component states. *A posteriori* reweighting, in the form of successive approximations character weighting (SACW) (Farris, 1969), was implemented using the rescaled consistency index of each character, to examine its effects on the stability of cladogram topology and the strength of branch support. Branch support was estimated by means of 1000 bootstrap replicates in PAUP (Felsenstein, 1985) (before and after SACW) and by calculating decay indices (Bremer, 1988, 1994) using the program AUTODECAY 4.0 (Eriksson, 1998) in combination with PAUP. Character distribution was studied using MacClade version 3.05 (Maddison & Maddison, 1995).

Morphological characters and observations

The thirty-five characters used in the phylogenetic analyses included one from adult ecology, four from the adult head, five from the adult body, six from wing venation and pattern, nine from male genitalia, one from female genitalia and nine from the ecology and morphology of early stages. Once more species have been reared, additional characters from the early stages will undoubtedly come to light, particularly concerning larval morphology and first-instar chaetotaxy. However, given the current dearth of available material, such characters used here must be treated as preliminary. All adult characters were coded using the type species of each genus (see Table 2) unless otherwise stated, but if the early stages were not known for the type species then relevant characters were coded using related species of that genus (even if currently misplaced). Generic autapomorphies were excluded, but those for Riodininae were included because they have not previously been published in a phylogenetic context. The consistency and retention indices given for each character are derived from the analysis presented here.

Table 2. Dissections examined for the phylogenetic analyses. The following collection acronyms are used: AME, Allyn Museum of Entomology, Florida Museum of Natural History, Sarasota; AMNH, American Museum of Natural History, New York; BMNH, The Natural History Museum, London; JHKW, Collection of Jason P. W. Hall and Keith R. Willmott, Washington; MNHN, Musée Nationale d'Histore Naturelle, Paris; USNM, National Museum of Natural History, Smithsonian Institution, Washington; ZMHU, Zoologische Museum für Naturkunde, Humboldt Universität, Berlin.

Taxon	Dissections examined
Euselasia aurantiaca (Salvin & Godman, 1868)	1♂, Guatemala, Guatemala, Ciudad de Guatemala (USNM); 1♀, Guatemalea, lzabal, Cayuga (USNM)
Alesa prema (Godart, [1824])	1♂, Brazil, Minas Gerais, Paracatu (USNM); 1♀, Brazil, Pernambuco, São Lourenço da Mata (USNM)
Eurybia halimede (Hübner, [1807])	1♂, French Guiana, Cayenne, Montsinéry (USNM); 1♀, French Guiana, Cayenne, Mount Mahoury (USNM)
Eunogyra satyrus Westwood, [1851]	2♂, Ecuador, Morona-Santiago, Bomboiza (JHKW); 1♀, Ecuador, Napo, Apuya (JHKW); 1♂, Peru, Loreto, Río Nanay, Puerto Almendra (USNM)
Teratophthalma phelina (C. & R. Felder, 1862)	1♂, Peru, Pasco, Río Chuchurras, Río Palcazu (BMNH); 1♀, Ecuador, Napo, Apuya (JHKW)
Leucochimona icare Hübner, [1819]	1♂, 1♀, Guyana, Upper Demerara-Berbice, Rockstone (USNM)
Perophthalma tullius (Fabricius, 1787)	1♂, 1♀, Panama, Veraguas, Santa Fé (USNM)
Mesophthalma idotea Westwood, [1851]	1♂, 1♀, Brazil, Rondônia, vicinity of Cacaulândia (USNM)
Semomesia croesus (Fabricius, 1776)	1♂, French Guiana, Cayenne, Saül (USNM); 1♀, French Guiana, Cayenne, Saint Élie (USNM)
Mesosemia philocles (Linnaeus, 1758)	1♂, 1♀, French Guiana, Cayenne, Vidal (USNM)
Hyphilaria nicia Hübner, [1819]	1♂, Peru, Loreto, Río Sucusari, Explornapo-ACEER (UNSM); 1♀, Brazil, Rondônia, vicinity of Cacaulândia (USNM)
Eucorna sanarita (Schaus, 1902)	1♂, Brazil, Rio de Janeiro, Parque Nacional de Itatiaia (USNM)
Voltinia radiata (Godman & Salvin, 1886)	1♂, 'Costa Rica' (BMNH); 1♂, Ecuador, Manabí, Palmar (AMNH); 1♀, Costa Rica, Limón, Guápiles (USNM)
Napaea eucharila (Bates, 1867)	1♂, Costa Rica, Cartago, Turrialba (USNM); 1♂, Panama, Chiriquí, Río Tolé (USNM); 1♂, Panama, Darién, Caña (USNM); 1♀, Panama, Colón, Río Guanche (USNM); 1♂, Venezuela, Carabobo, Puerto Cabello (ZMHU); 1♂, Venezuela, Amazonas, Cerro Marahuaca (ZMHU); 1♂, Colombia, Meta, Río Negro (USNM); 1♂, Ecuador, Pichincha, Alluriquín (USNM); 1♂, Peru, Loreto, Iquitos (MNHN); 1♂, Bolivia, La Paz, Río Songo (ZMHU); 1♂, Brazil, Pará, 15 km. S of Itaituba (USNM); 1♀, Paraguay, Paraguarí, Sapucay (BMNH); 1♂, French Guiana, Cayenne, Galion (USNM); 1♂, French Guiana, Cayenne, Remire (USNM)
Cremna actoris (Cramer, 1776)	1♂, Peru, Madre de Dios, 30 km. WSW of Puerto Maldonado (USNM); 1♂, Brazil, Mato Grosso, Diamantino (USNM), 1♂, French Guiana, Cayenne, Matoury (USNM); 1♀, French Guiana, Saint Laurent du Maroni, 10 km. W of Charvein (USNM)
Hermathena candidata Hewitson, 1874	1♂, Colombia, Cauca, Pescador (AME); 1♂, Ecuador, Zamora-Chinchipe, Qbda. de Chorillos, nr Zamora (JHKW); 1♂, Peru, Pasco, Oxapampa (MNHN)
Ithomiola floralis C. & R. Felder, 1865	1♂, Panama, Darién, Cerro Pirre (USNM); 1♂, Colombia, Boyacá, Muzo (AME); 1♂, Colombia, Meta, Río Negro (USNM); 1♂, Ecuador, Pastaza, km 25 Puyo-Tena Rd. (USNM); 2♂, Ecuador, Pastaza, Puyo (AME); 1♂, Peru, Loreto, Río Sucusari, Explornapo-ACEER (USNM); 1♂, Peru, Loreto, Iquitos (AME); 1♂, Guyana, Potaro-Siparuni, Kaiteur Falls (USNM); 1 ♀, Guyana, Potaro-Siparuni, Tumatumari (USNM); 1♂, French Guiana, Cayenne, Roura (USNM)
Riodina lysippoides Berg, 1882	1♂, Argentina, Tucumán, Tucumán (USNM); 1♀, Uruguay, Florida, Durazno (USNM)
Esthemopsis colaxes (Hewitson, 1870)	1♂, Panama, Canal Zone, Piña (USNM); 1♀, Panama, Panamá, Bayano (USNM)

Adult ecology

1. *Butterflies rest with wings*: (0) closed (Fig. 2A); (1) half open (Fig. 2B); (2) fully open (Fig. 2C). CI = 1; RI = 1.

Character states were assigned based on personal field observations. Resting with the wings open is generally characteristic of Riodininae. Resting with wings closed is universal for Euselasiinae, but present elsewhere in only a few genera of the riodinine tribes Helicopini and Nymphidiini (Hall, 1998, 2002). Resting with the wings half open is found in the Old World Nemeobiinae and most genera of Riodininae with five FRV.

Adult head

2. *Eyes*: (0) bare; (1) setose. CI = 1; RI = 1.

The distribution of bare vs setose eyes in the five FRV group of genera was correctly reported by Harvey (1987). Setose eyes appear to be universal in those genera indicated. It should also be noted that all members of genera scored with state (0) have bare eyes, with only one exception. As well as possessing setose eyes, *Hyphilaria anophthalma* (C. & R. Felder, 1865) has genitalia typical of the *Mesosemia* group of genera, to which it eventually needs to be transferred (Hall & Harvey, unpublished).

3. *Metallic gloss to living eyes*: (0) absent; (1) present. CI = 1; RI = 1.

This character for *Eurybia* and *Alesa* is well known to field workers, and was noted by DeVries (1997). Although the metallic gloss is particularly brilliant in living individuals, the character is still evident in most pinned specimens.

4. *Pale scaling at margin of eyes*: (0) continuous; (1) broken dorsolaterally. CI = 1; RI = 1.
5. *Bristlelike scales on medial surface of palpi*: (0) absent; (1) present (Fig. 3A). CI = 1; RI = 1.

This was the primary character used by Harvey (1987) to define his Eurybiini. The bristles are present on the first and second palpal segments in *Eurybia*, but on the first segment only in *Alesa*.

Fig. 2. Riodinid resting postures. Photographs by Keith Willmott (A,B) and Jim Mallet (C). A, *Euselasia serapis*, wings closed over body (ch. 1 : 0); B, *Mesosemia visenda*, wings half open (ch. 1 : 1); C, *Eurybia dardus*, wings outspread (ch. 1 : 2).

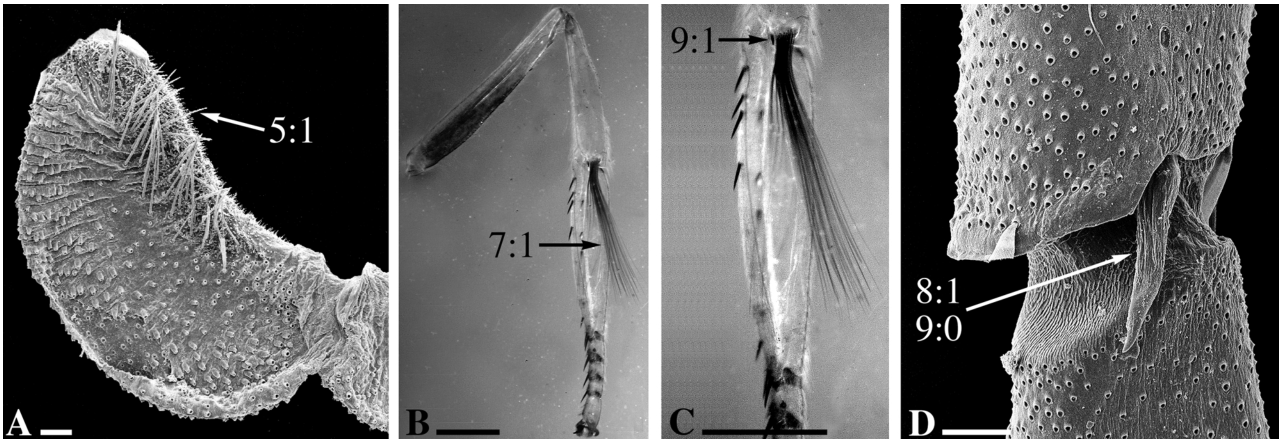

Fig. 3. Male appendages. A, *Alesa prema*, lateral view of first palpal segment illustrating medial spines; B,C, '*Napaea*' *neildi*, lateral view of male hindleg illustrating hairpencils and small tibial spur; D, '*Napaea*' *theages*, lateral view of male hindleg illustrating large tibial spur. Scales = 50 µm (A,D), 0.5 mm (B,C).

Adult body

6. *Tibia and tarsus of male foreleg*: (0) separate (Fig. 4J); (1) completely or partially fused (Fig. 4K). CI = 1; RI = 1.

The complete or partial fusion of the tibia and tarsus of the male foreleg was illustrated and used by Stichel (1910–1911) to divide his Eurybiini into Semomesiina, whose species possess this character, and Eurybiina, whose species did not.

7. *Hairpencils on male hindleg*: (0) absent; (1) present (Fig. 3B,C). CI = 1; RI = 1.

The presence of male leg hairpencils in certain five FRV genera of Riodininae was first reported by Hall & Harvey (2002). Similar structures are not known elsewhere in Papilionoidea, but are relatively common in Hesperioidea (Müller, 1877; Evans, 1949). They occur in twelve species of *Ithomiola* (all species), *Hermathena* (all species), the '*Napaea*' *nepos* group (majority of species; these appear to belong to *Ithomiola*) and '*Cremna*' (*thasus* Stoll, [1780], and *alector* Geyer, 1837, only; neither are closely related to the type species of *Cremna*). The setae are inserted at the inner distal tip of a shortened tibia and lie within a pouch along the inner edge of a lengthened first tarsal segment. The pouch is lined with sparsely distributed oval, ribbed and presumably pheromone releasing scales. The hairpencil sockets are medially constricted, suggesting the shaft can be kept in repose or erect, and the shafts are ribbed in cross-section and filled with spongy trabeculae, suggesting efficient storage and dissemination of pheromones (Hall & Harvey, 2002).

8. *Tibial spur on male hindleg*: (0) present (Fig. 3C,D); (1) absent. CI = 0.33; RI = 0.75.

Most Papilionoidea have a pair of spurs on the tibiae of mid- and hindlegs, although this pair has been lost independently in many groups (e.g. Clench, 1955; Eliot, 1973). Riodinidae are very unusual in generally having only a single anterior spur (Harvey, 1987). The complete absence of tibial spurs in the family occurs sporadically in Nemeobiinae, Euselasiinae and apparently only those ingroup genera of Riodininae indicated (Harvey, 1987). Tibial spurs are consistently either present or absent in most of the ingroup genera treated here, but there is variation within *Napaea* (the *nepos* group, which has closer phylogenetic affinities to *Ithomiola* than to the *N. eucharila* group, has tibial spurs) and *Eurybia*. As most of the species examined in the latter (unequivocally monophyletic) genus have tibial spurs, *Eurybia* is coded with state (0), even though its type species exhibits state (1).

9. *If tibial spur on male hindleg present (8 : 0), spur*: (0) large (Fig. 3D); (1) small (Fig. 3C). CI = 1; RI = 1.

It is possible that the presence of a small tibial spur in *Ithomiola* and *Hermathena* species is correlated with the presence of hairpencil sockets in the same distal region of the tibia.

10. *Four pale spots on dorsal surface of thorax*: (0) absent; (1) present (Fig. 1M). CI = 1; RI = 1.

Four isolated pale thoracic spots are present in all *Cremna* (except the misplaced *thasus* and *alector*) and most *Napaea* species. The *phryxe* group of *Napaea*, whose phylogenetic affinities with respect to the *eucharila* group are currently uncertain, lack such spots.

Wing venation and pattern

11. *Number of forewing radial veins*: (0) 5; (1) 4 (see illustrations in Stichel, 1910–1911). CI = 0.5; RI = 0.67.

The number of forewing radial veins has always been an important element of higher-level riodinid classifications (see Introduction). All Nemeobiinae and most Euselasiinae possess five FRV. However, some *Euselasia* species have males with three or four FRV, and those males with five FRV have females with only four (Stichel, 1928; Harvey, 1987).

12. *Cross vein between forewing radial veins Sc and R1*: (0) absent; (1) present (see illustrations in Stichel, 1910–1911). CI = 0.5; RI = 0.

The presence of a cross vein between forewing radial veins Sc and R1 was used by Stichel (1910–1911) (before he had the opportunity to examine the then recently described *Eucorna sanarita*) to delimit membership of *Cremna*. However, phylogenetic studies of Theopeina (Hall, 1999, 2002) and the *Napaea* group of genera (Hall & Harvey, unpublished), indicate that this character is highly homoplasious.

13. *Costal vein on hindwing*: (0) absent; (1) present (see illustrations in Stichel, 1910–1911). CI = 1; RI = 0.

The presence of a costal vein at the basal margin of the hindwing was one of the characters used by Harvey (1987) to define Riodininae.

14. *Eyespot containing plain pale pupils immediately before forewing discal cell end*: (0) absent (e.g. Fig. 1C); (1) present (e.g. Fig. 1I). CI = 0.5; RI = 0.75.

The eyespots of *Perophthalma*, which are positioned distal of the discal cell end, and *Eurybia*, which have iridescent blue pupils, are not believed to be homologous with those of taxa coded with state (1).

15. *Multiple symmetrical narrow bands (*i.e. > *5)*: (0) absent (e.g. Fig. 1C); (1) present (e.g. Fig. 1F). CI = 1; RI = 1.
16. *Even brown and white chequering on forewing fringe*: (0) absent (e.g. Fig. 1O); (1) present (e.g. Fig. 1M). CI = 1; RI = 1.

Male genitalia

17. *Genital capsule*: (0) approximately vertical (angle of vinculum > 60°) (e.g. Fig. 4C); (1) posteriorly inclined (angle of vinculum < 60°) (Fig. 4A). CI = 0.1; RI = 1.
18. *Lateral windows of tegumen*: (0) separate (e.g. Fig. 4B); (1) narrowly fused dorsally (Fig. 4I). CI = 0.5; RI = 0.88.
19. *Small bulbous lateral swelling at ventral margin of lateral window in tegumen*: (0) absent (Fig. 4B); (1) present (e.g. Fig. 4E). CI = 1; RI = 1.

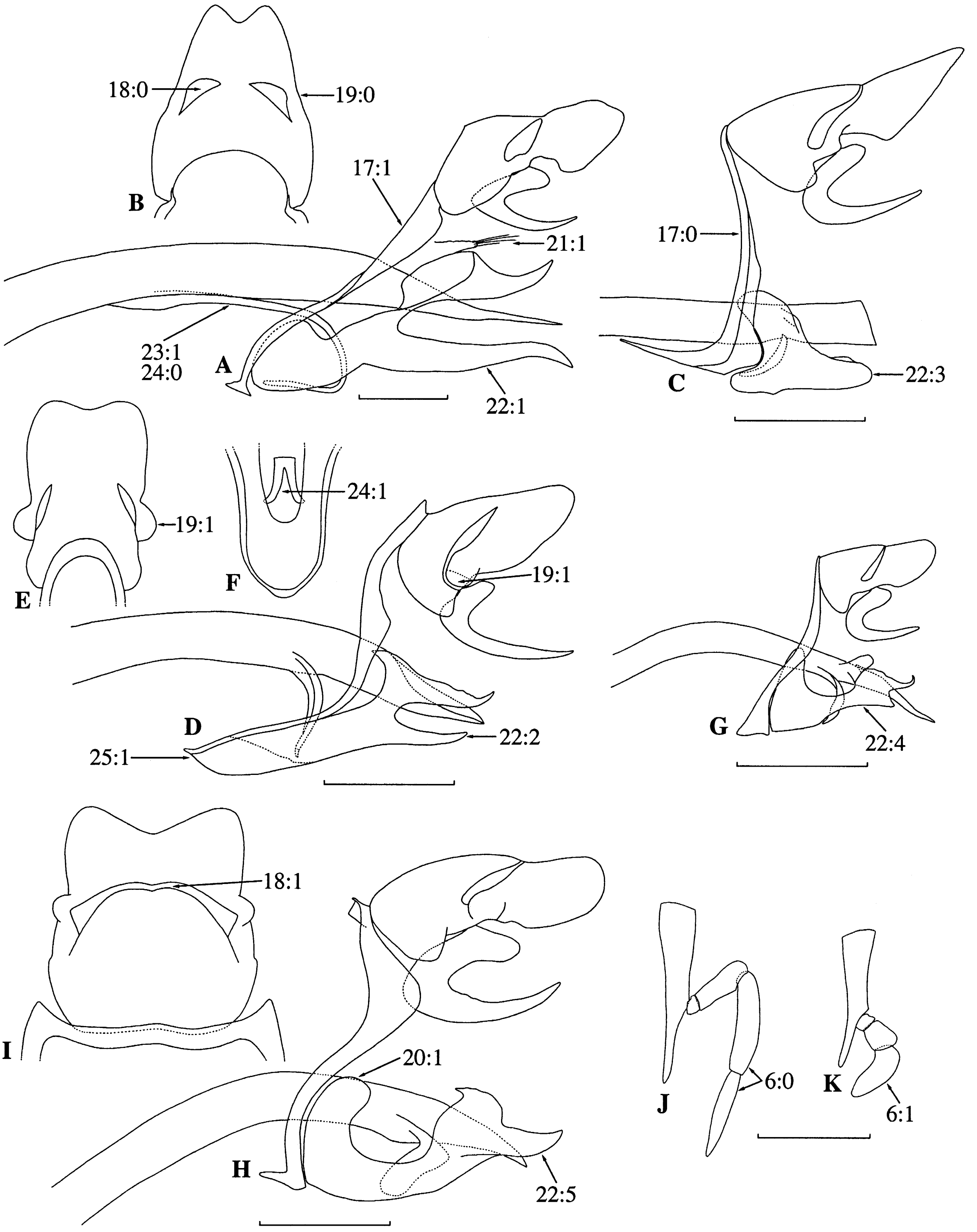

Fig. 4. Male genitalia and appendages. Lateral view of male genitalia (A,C,D,G,H), dorsal view of uncus (B,E,I), ventral view of base of valvae (F) and male forelegs in lateral view (J,K). Aedeagal cornuti are omitted for clarity. A,B, *Eurybia halimede*; C, *Eunogyra satyrus*; D–F, *Mesosemia philocles*; G, *Hyphilaria nicia*; H,I, *Napaea eucharila*; J, *Mesosemia philocles*; K, *Semomesia croesus*. Scales = 0.5 mm.

State (1) was present in all species examined for the genera indicated and is not known elsewhere in the subfamily. It is most prominent in the *Mesosemia* group of genera.

20. *Anteriolateral sclerotized bulge on valvae*: (0) absent (e.g. Fig. 4D); (1) present (e.g. Fig. 4H). CI = 1; RI = 1.
21. *Setae on transtilla*: (0) absent; (1) present (Fig. 4A). CI = 1; RI = 1.
22. *Valvae*: (0) elongate and roundly triangular; (1) posteriorly elongate with upper, lower and outer projections (Fig. 4A); (2) triangular with 2 well separated and typically parallel posterior projections and narrow intervening section (Fig. 4D); (3) stoutly triangular with rounded ventral margin and concave anterior margin (Fig. 4C); (4) triangular with upwardly pointed posterior tip and small setose and weakly sclerotized basal projection (Fig. 4G); (5) rectangular with typically elongate posterior projection from lower posterior corner (Fig. 4H); (6) a dorsoventrally flattened plate over aedeagus; (7) divided into 2 elongate and rounded projections with inner process supporting aedeagus. CI = 1; RI = 1.
23. *Pedicel*: (0) absent; (1) present (e.g. Fig. 4A). CI = 1; RI = 0.

The presence of a male genital pedicel connecting the aedeagus to the base of the valvae was one of the characters used by Harvey (1987) to define Riodininae.

24. *Pedicel*: (0) entire (e.g. Fig. 4A); (1) medially desclerotized, ventrally split or both (Fig. 4F). CI = 1; RI = 1.

Harvey (1987) used the presence of a medially desclerotized male genital pedicel that splits into two at its connection with the valvae to redefine his Mesosemiini. However, although he originally included only *Perophthalma*, *Mesophthalma*, *Leucochimona*, *Semomesia* and *Mesosemia* in that tribe, character state (1) is also present in *Eunogyra* and *Teratophthalma*. A ventrally split pedicel has been independently derived in certain genera of Nymphidiini (Harvey, 1987; Hall & Harvey, 2001) and a very faint medial desclerotization only of the pedicel is present in certain *Hyphilaria* and *Napaea* species.

25. *Anteriorly elongate and dorsally concave saccus*: (0) absent; (1) present (e.g. Fig. 4D). CI = 1; RI = 1.

Female genitalia

26. *Signa*: (0) approximately opposite each other (Fig. 5B,D); (1) in same half of corpus bursae (Fig. 5A,C). CI = 1; RI = 1.

Character state (1) is rare in Riodinidae, but occurs elsewhere in, for example, a derived group of *Nymphidium* (Hall, unpublished).

Ecology and morphology of early stages

27. *Larvae feed on*: (0) Clusiaceae; (1) Marantaceae; (2) Rubiaceae; (3) Araceae; (4) epiphytes (Bromeliaceae and Orchidaceae). CI = 1; RI = 1.

Foodplant data are based on the following sources: Zikán (1920, 1953), Beutelspacher (1972), Biezanko *et al.* (1979), Harvey (1987), Horvitz *et al.* (1987), Bullock (1990), Brévignon (1992, 1993), Callaghan (1993), DeVries *et al.* (1994), DeVries (1997), Brévignon & Gallard (1997, 1999), Meerman (1999), Janzen & Hallwachs (2002) and D. J. Harvey, personal communication. States (0) and (3) apply to the taxa specified in Table 2 only, but repeated *bona fide* rearings indicate states (1), (2) and (4) to be the predominant if not exclusive foodplants for the genera indicated. *Alesa* is given a '?' because the larvae are carnivorous on homopteran nymphs (DeVries & Penz, 2000).

28. *Tentacle nectary organs at junction of larval abdominal segments 8 and 9*: (0) absent; (1) present (Fig. 6A). CI = 1; RI = 0.

Dorsal tubelike paired tentacle nectary organs (*sensu* Cottrell, 1984) at the junction of the eighth and ninth larval abdominal segments are known in all reared species of *Alesa* and *Eurybia* (Harvey, 1987; Horvitz *et al.*, 1987; DeVries, 1997; DeVries & Penz, 2000; D. J. Harvey, personal communication). These organs, which secrete nutritionally

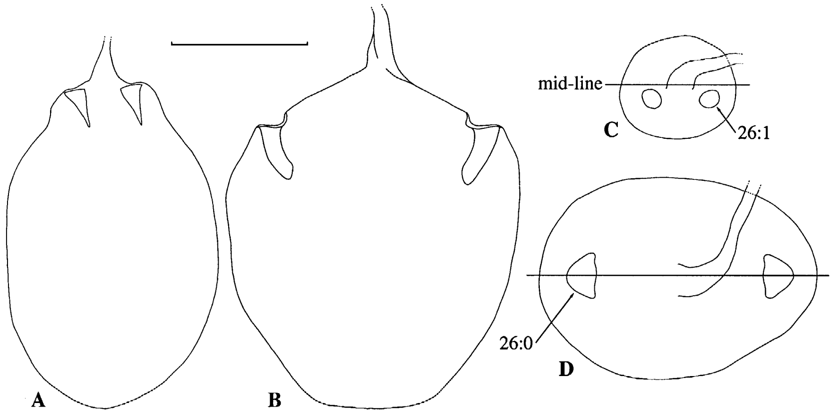

Fig. 5. Female genitalia. Corpus bursae in lateral (A,B) and ventral (C,D) views. A,C, *Napaea eucharila*; B,D, *Mesosemia philocles*. Scale = 1 mm.

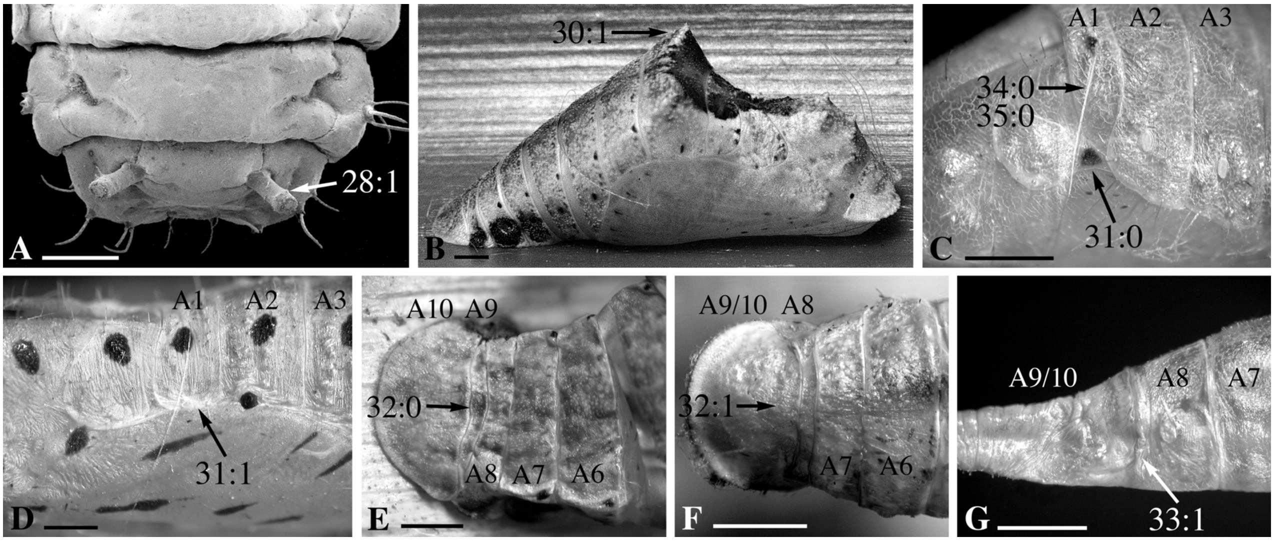

Fig. 6. Early stages. Dorsal view of posterior portion of larva (A), lateral view of entire (B), medial (C,D) or posterior portion (G) of pupa, and dorsal view of posterior portion of pupa (E,F). A, *Alesa rothschildi*; B, *Napaea umbra*; C, *Euselasia midas*; D, *Stalachtis phlegia*; E, *Napaea eucharila*; F, *Synargis abaris*; G, *Eurybia lycisca*. Scales = 1 mm.

rich droplets to be harvested by ants (DeVries, 1988; DeVries & Baker, 1989), were originally noted by Guppy (1904) for the genera *Theope* Doubleday, 1847, and *Juditha* Hemming, 1964, and they have since been reported on all myrmecophilous larvae (i.e. those in Eurybiini and Nymphidiini) (Harvey, 1987; DeVries, 1997). The character was one of those used by Harvey (1987) to define Eurybiini.

29. *Anteroventral displacement of spiracle on larval abdominal segment 1*: (0) absent; (1) present (see illustrations in Stehr, 1987: 447). CI = 1; RI = 0.

The anteroventral displacement of the spiracle on larval abdominal segment one was a character used by Harvey (1987) to define Riodininae. Species whose larvae have been examined for this character are listed in Appendix 1 of Harvey (1987). Characters 29–31 and 34–35 were coded for *Hyphilaria* and *Ithomiola* based on the illustrations and descriptions of *thasus* and *nepos* early stages given by DeVries (1997) and Callaghan (1993), respectively. Although these two species are not currently treated in *Hyphilaria* and *Ithomiola*, preliminary phylogenetic study indicates that they are closely related to the type species of those genera (Hall & Harvey, unpublished).

30. *Prominent crest on pupal abdominal segment 2*: (0) absent; (1) present (Fig. 6B). CI = 0.5; RI = 0.8.

This pupal character was noted by Harvey (1987) as being typical of *Mesosemia* and *Napaea* group genera. Species whose pupae have been examined for chs 30–31 and 34–35 are listed in Appendix 2 of Harvey (1987).

31. *Abdominal pupal segment 1*: (0) partially separated from mesothorax (Fig. 6C); (1) entirely in contact with mesothorax (Fig. 6D). CI = 1; RI = 0.

The contact between pupal abdominal segment one and the mesothorax was a character used by Harvey (1987) to define Riodininae.

32. *Ninth pupal abdominal segment*: (0) separate (Fig. 6E); (1) fused with segment 10 (Fig. 6F). CI = 1; RI = 1.

The ninth segment was completely fused with the tenth in all examined pupae of the four FRV tribes of Riodininae, with the exception of the single examined symmachiine pupa, in which the segments were fused only dorsally. Species whose pupae have been examined for characters 32–33, which included representatives from all the recognized tribes, are listed in Appendix 2.

33. *Intersegmental membrane between eighth and ninth pupal abdominal segments*: (0) complete; (1) confined to dorsum (Fig. 6G). CI = 1; RI = 1.
34. *Silk girdle on pupa*: (0) present (e.g. Fig. 6C); (1) absent (Fig. 6B). CI = 1; RI = 1.

Most pupae of Papilionoidea possess a silk girdle, but it is universally absent in Nymphalidae and sporadically absent in Lycaenidae and Riodinidae (Harvey, 1987). Its absence in *Napaea* was first noted by Harvey (1987), and subsequent rearings of related genera (Brévignon, 1992; Callaghan, 1993; J. Rawlins, personal communication) would appear to confirm the frequent absence of a girdle in the *Napaea* group of genera. However, there is still too little information to assess how widespread its absence might be within genera of this group. For example, Brévignon (1992) indicates the presence of a silk girdle in his illustration of the pupa of *Napaea beltiana* (Bates, 1867).

35. *If silk girdle on pupa present (34 : 0), girdle crosses abdominal segment*: (0) 1 (e.g. Fig. 6C); (1) 2. CI = 1; RI = 1.

The typical condition in Riodinidae is for the silk girdle to cross abdominal segment one (Harvey, 1987). The presence of a silk girdle crossing abdominal segment two was first noted as being characteristic for the *Mesosemia* group of genera by Harvey (1987).

Results and discussion

Both equally weighted and successively weighted analyses of the dataset in Appendix 1 generated five equally most parsimonious cladograms (MPCs) (equal weights: length = 54; CI = 0.87; RI = 0.93; SACW: length = 44.84; CI = 0.96; RI = 0.98). The strict consensus of these is shown in Figs 7 and 8. Once SACW has down-weighted the most homoplasious characters, the bootstrap values for the nodes uniting subtribes Mesosemiina and Napaeina, respectively, are about ten points higher.

Riodininae

The monophyly of Riodininae is strongly supported by one character from wing venation, one from male genitalia and one each from larval and pupal morphology. Although first reported by Harvey (1987), these characters are discussed here for the first time in a published work.

The presence of a costal vein at the basal margin of the hindwing is unique within Papilionoidea to this subfamily, where it is present in all genera except *Helicopis* Fabricius, 1807. The clear relationship between *Helicopis* (excluded from Riodininae by Stichel, 1910–1911, 1930–1931, but returned to that subfamily by Harvey, 1987) and other genera in Helicopini (Hall, 1998), indicates a secondary loss of the vein in that genus. A pedicel, or sclerotized ribbon, connecting the aedeagus to the base of the valvae in the male genitalia is present in all species of Riodininae and absent in all species of Nemeobiinae and Euselasiinae, except for a very weak pedicel-like structure in *Hades* Westwood, [1851]. In most larvae of Papilionoidea, including those of the riodinid subfamilies Nemeobiinae and Euselasiinae, the spiracle on abdominal segment one is in line with that on segment 2. However, in larvae of Riodininae, the spiracle on abdominal segment one is displaced anteroventrally. In the most extreme condition, found in the nymphidiine subtribes Nymphidiina and Theopeina, the spiracle is displaced to the ventral surface of the larva (Harvey, 1987; Hall, 1999, 2002).

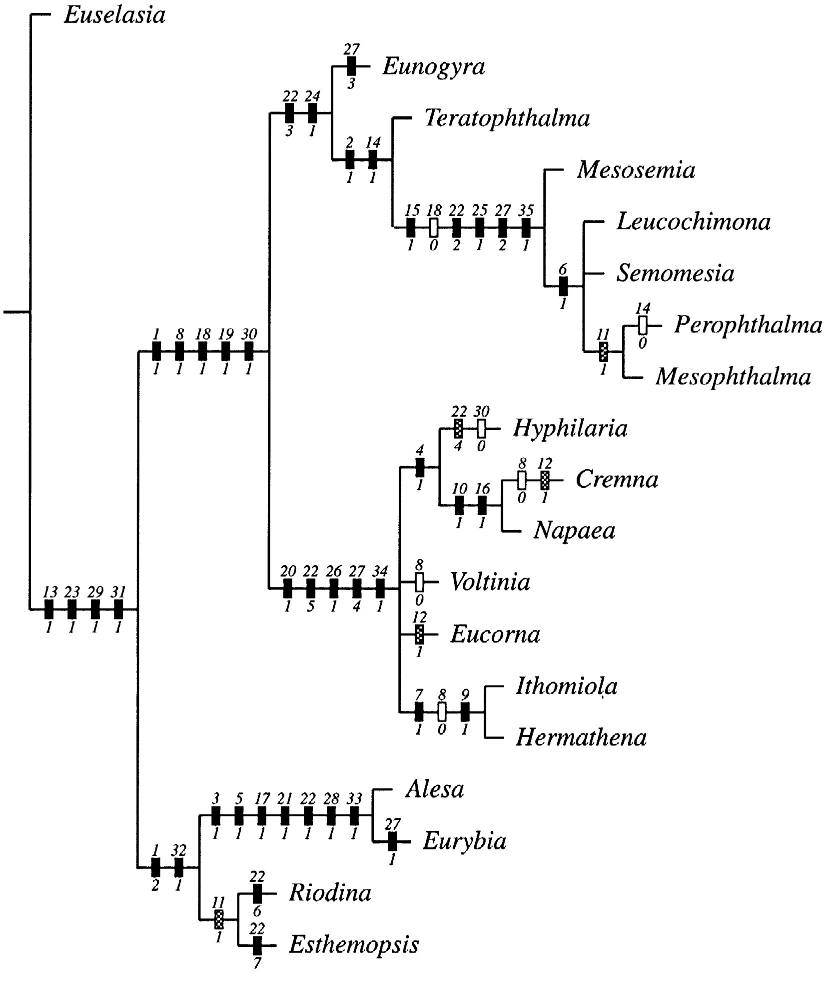

Fig. 7. Strict consensus of five equally most parsimonious cladograms, illustrating distribution of character states. Black bars indicate unique apomorphies, shaded bars homoplasious apomorphies and white bars reversals.

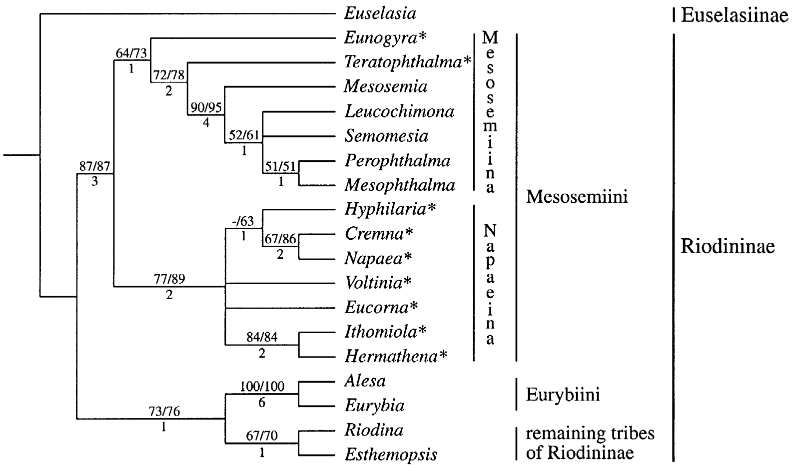

Fig. 8. Cladogram from Fig. 7 illustrating limits of subtribes, tribes and families. Branch support is given in the form of bootstrap values above branches (based on analysis using equal weights at left and SACW at right) and decay index values below branches. Asterisks indicate genera that were treated by Harvey (1987) in an *incertae sedis* section.

Finally, in all families of Papilionoidea except Lycaenidae and Riodinidae, pupal abdominal segment 2 is completely separated from the mesothorax by the metathorax, but in those two families the metathoracic wing case is reduced so that abdominal segment 2 contacts the mesothorax. In Riodininae, abdominal segment one additionally contacts the mesothorax (Harvey, 1987).

Eurybiini

The presence of bristles on the medial surface of palpi was first noted by Reuter (1896) for *Eurybia* in his comprehensive study of the palpi of butterflies, and used by him to propose the tribe Eurybiini. Stichel (1910–1911, 1930–1931) subsequently recognized Eurybiini to include all riodinine genera with five FRV (see Table 1), dividing it into Semomesiina, containing *Perophthalma*, *Mesophthalma*, *Leucochimona* and *Semomesia*, and Eurybiina, containing the remaining genera. Semomesiina was defined by its members having a short and swollen femur to the male foreleg, a character not used here because discrete states could not be discerned, and fused tibiae and tarsi of the male foreleg. Eurybiina was apparently delimited on the basis of its members not exhibiting these characters. Even though Stichel (1910–1911) had examined the male genitalia and appendages for exemplars of all five FRV genera, there is a great disparity between his ideas on intergeneric relationships in the group (as implied by the order in which genera were listed in his catalogues; see Table 1) and those outlined here (see Figs 7 and 8). Most recently, Harvey (1987) redefined Eurybiini to include *Eurybia* and *Alesa* only, on the basis of Reuter's original palpal character, which does not occur elsewhere in Riodinidae, and the presence of tentacle nectary organs (TNOs) on larval abdominal segment eight, which occur elsewhere only in Nymphidiini (as presumably independently derived structures) (Harvey, 1987).

In the phylogenetic analysis presented here, the monophyly of Eurybiini as conceived by Harvey (1987) is confirmed, and an additional five synapomorphies are given for the tribe (see Table 3). Eurybiini is most strongly supported by the aforementioned palpal character, the metallic bluish-green gloss to the adult eyes, the presence of TNOs on the larvae and the dorsal confinement of the intersegmental membrane between the eighth and ninth abdominal segments of the pupa.

Mesosemiini

Harvey (1987) recognized tribe Mesosemiini for Stichel's (1910–1911, 1930–1931) Semomesiina plus *Mesosemia*, primarily on the basis of its members possessing a ventrally divided male genital pedicel, but also secondarily setose eyes, the silk girdle of the pupa crossing abdominal segment 2 and the absence of tibial spurs. The remaining genera of Stichel's Eurybiina, minus *Eurybia* and *Alesa*, were placed by Harvey (1987) in an *incertae sedis* section with uncertain phylogenetic affinities, and many acknowledged to possess some of the secondary characters listed above for his Mesosemiini.

The monophyly of Harvey's (1987) Mesosemiini is confirmed here. However, confidence in the topology within this section of the cladogram is not high, largely because of uncertainty concerning the monophyly of the two largest genera, *Mesosemia* and *Semomesia*. For example, it is quite possible that the derived foreleg condition used by Stichel (1910–1911) to unite *Perophthalma*, *Mesophthalma*, *Leucochimona* and *Semomesia* was derived from a *Mesosemia*-like ancestor. It is also not clear, based on other characters, that the presence of only four FRV in *Perophthalma* and *Mesophthalma* is an indicator of their joint monophyly. Detailed species-level study of this group of genera is

Table 3. Synapomorphies for the five forewing radial-veined tribes and subtribes of Riodininae. The numbers in brackets after each taxon represent the number of species it contains, and the numbers in brackets after each apomorphy refer to the character number and state in this study. Reference is given to figure numbers where appropriate.

Family group taxon	Synapomorphies
Eurybiini [*c.* 33]	Metallic bluish-green gloss to living eyes [3 : 1]
	Bristlelike scales on medial surface of palpi [5 : 1] (Fig. 3A)
	Male genital capsule posteriorly directed (angle of vinculum < 60°) [17 : 1] (Fig. 4A)
	Setae present on male genital transtilla [21 : 1] (Fig. 4A)
	Male genital valvae elongate with upper, lower and outer projections at posterior tip [22 : 1] (Fig. 4A)
	Tentacle nectary organs on larval abdominal segment 8 [28 : 1] (Fig. 6A)
	Intersegmental membrane between eighth and ninth pupal abdominal segments confined to dorsum [33 : 1] (Fig. 6G)
Mesosemiini [*c.* 182]	Adults rest with wings half open [1 : 1] (Fig. 2B)
	Hindleg tibial spur absent [8 : 1] (present in *Cremna*, *Voltinia*, *Ithomiola* and *Hermathena*)
	Lateral windows of male genital tegumen narrowly fused dorsally [19 : 1] (Fig. 4I) (not present in *Mesosemia* group of genera)
	Small bulbous lateral swelling at ventral margin of lateral windows in male genital tegumen [19 : 1] (e.g. Fig. 4E)
	Prominent crest on pupal abdominal segment 2 [30 : 1] (Fig. 6B) (not present in *Hyphilaria*)
Mesosemiina [*c.* 140]	Eyes setose [2 : 1] (not present in *Eunogyra*)
	Eyespot immediately before forewing discal cell end [14 : 1] (e.g. Fig. 1I) (not present in *Eunogyra* and *Perophthalma*)
	Multiple narrow bands on wings [15 : 1] (e.g. Fig. 1F) (not present in *Eunogyra* and *Teratophthalma*)
	Male genital valvae triangular with 2 well separated and typically parallel posterior projections and narrow intervening section [22 : 2] (Fig. 4D) (not present in *Eunogyra* and *Teratophthalma*)
	Male genital pedicel split and or medially desclerotized or both [24 : 1] (Fig. 4F)
	Larvae feed on plants in Rubiaceae [27 : 2] (not *Eunogyra*)
	Silk girdle on pupa crosses abdominal segment 2 [35 : 1]
Napaeina [42]	Prominent anterior bulge in male genital valvae [20 : 1] (e.g. Fig. 4H)
	Male genital valvae rectangular with typically elongate posterior projection from lower posterior corner [22 : 5] (Fig. 4H) (not *Hyphilaria*)
	Female genital signa positioned in same half of corpus bursae (Fig. 5A,C) [26 : 1]
	Larvae feed on epiphytic bromeliads and orchids [27 : 4]
	Silk girdle on pupa absent [34 : 1] (Fig. 6B)

needed before stable and natural generic groupings can be established.

The most interesting result of the analyses is the indication of three previously unrecognized higher-level monophyla within the five FRV group of genera that have good character support (see Table 3) and branch support after SACW. It is suggested that Harvey's (1987) Mesosemiini plus *Eunogyra* and *Teratophthalma*, his *incertae sedis* section without these two genera, and these two generic groupings together all constitute monophyletic groups. The most convincing characters supporting the monophyly of the first group, which is henceforth referred to as Mesosemiina, are a medially desclerotized and ventrally split male genital pedicel (scored incorrectly for *Eunogyra* and *Teratophthalma* by Harvey, 1987) and setose eyes (all genera except *Eunogyra*). Only time will tell how ubiquitous the two potentially strong early stage characters will be, namely that the larvae of all reared genera except *Eunogyra* feed on Rubiaceae (Zikán, 1953; Biezanko *et al.*, 1979; Harvey, 1987; DeVries *et al.*, 1994; DeVries, 1997; Janzen & Hallwachs, 2002), and the silk girdle on pupae crosses abdominal segment 2 instead of one. Early stage material for the two basal genera of Mesosemiina, *Eunogyra* and *Teratophthalma*, should further clarify their true phylogenetic position.

The new subtribal name Napaeina is here proposed for Harvey's (1987) *incertae sedis* section without *Eunogyra* and *Teratophthalma*. *Napaea* is designated as the type genus, and the remaining included genera are *Hyphilaria*, *Eucorna* (= the preoccupied names *Eucora* Schaus, 1902 and *Eucorma* Seitz, 1924), *Voltinia*, *Cremna*, *Ithomiola* (= *Compsoteria* Hewitson, 1870) and *Hermathena*. These genera, of which the largest, *Napaea*, appears to be a polyphyletic assemblage as currently conceived, contain forty-two species, including several that are undescribed (Hall & Harvey, unpublished). The most convincing synapomorphies for Napaeina are the form of the male genital valvae, which are rectangular with a large medial desclerotized region dorsally, a prominent anterior bulge and typically an elongate posterior projection from the lower posterior corner, female genital signa asymmetrically positioned in the same half of the corpus bursae, and all known larval foodplants being epiphytic Bromeliaceae and Orchidaceae (Zikán, 1920; Beutelspacher, 1972; Biezanko *et al.*, 1979; Bullock, 1990; Brévignon, 1992, 1993; Callaghan, 1993; DeVries *et al.*, 1994; Brévignon & Gallard, 1997, 1999;

DeVries, 1997; Meerman, 1999; Janzen & Hallwachs, 2002). Although insufficient material was available to include meaningfully the following characters in the analysis, the known larvae of Napaeina species appear to all be densely covered in long and curved whitish setae, whereas those of Mesosemiina are generally more sparsely covered with straight and dark setae, and the pupae of Napaeina species lack the elaborate setae on the anterior ridges of the pupae of Mesosemiina species (see illustrations in DeVries, 1997). Additionally, the presence of spines at the vertices of the hexagonal sculpturing on the known eggs of Mesosemiina (e.g. see illustrations in DeVries, 1997), with the aeropyles along the ridges between them, may well prove to be a phylogenetially informative character within Mesosemiini. No eggs have been seen for Napaeina genera.

A more broadly defined Mesosemiini is proposed here that includes all genera of Riodininae with five FRV except the two genera of Eurybiini. The monophyly of this clade is most convincingly supported by the small bulbous lateral swelling at the ventral margins of the lateral windows in the male genital tegumen, a character not known from the remainder of Riodininae. The perching posture of these species, with the wings half open, is similarly not known elsewhere in any large group of Riodininae, but it is also characteristic of the Old World Nemeobiinae. The presence of a prominent crest on pupal abdominal segment two in almost all reared genera of Mesosemiini (Harvey, 1987) is currently the only early stage character for the tribe, but more are expected when more material becomes available.

Relationship between tribes of Riodininae with four and five forewing radial veins

Stichel (1910–1911, 1930–1931) included all genera of Riodininae with five FRV in Eurybiini, implicitly implying that they were more closely related to each other than any other genera (all with four FRV) in the subfamily. However, this character is a symplesiomorphy, occurring throughout Nemeobiinae and Euselasiinae. Subsequently, in the first tentative phylogeny presented for Riodinidae, Harvey (1987) treated his three groups of five FRV genera as part of an unresolved quadrichotomy, with the fourth clade comprising all genera with four FRV. DeVries (1997) attempted to translate Harvey's (1987) character list into a data matrix for analysis using explicit cladistic methodology, but as that matrix contained numerous errors, his results are relatively meaningless and are not discussed any further.

A new character is reported here, the fusion of pupal abdominal segments 9 and 10, that appears to unite Eurybiini with all the four FRV tribes of Riodininae. All pupae examined in Nemeobiinae, Euselasiinae and the more broadly conceived Mesosemiini have these segments separate, and those examined for the remainder, including representatives from all the recognized four FRV riodinine tribes, have them fused. Species whose pupae have been examined are listed in Appendix 2. Although the examination of pupae for more species and further corroborating characters are clearly desirable, and a more detailed understanding of the morphology and phylogenetic relationships among all the four FRV tribes is needed before firmer conclusions can be drawn, Mesosemiini + (Eurybiini + all four FRV tribes) is tentatively suggested as the best current hypothesis of how the five and four FRV tribes are related to each other. Although the loss of one forewing radial vein still constitutes the sole character uniting the majority of tribes in Riodininae, no convincing evidence has thus far been found to contradict the hypothesis of their collective monophyly.

Acknowledgements

I thank those who gave me access to the riodinid collections in their care and facilitated the loan of specimens, including: Phillip Ackery (BMNH), Wolfram Mey (ZMHU), Lee and Jacqueline Miller (AME) and Jacques Pierre (MNHN); the following for the financial assistance of field and museum research, including: Oxford University (Poulton Fund), Cambridge University (Christ's College), The Royal Entomological Society, Sigma Xi, Equafor, The National Geographic Society (Research and Exploration Grant #5751-96), the Smithsonian Institution (two postdoctoral fellowships) and the National Science Foundation (DEB #0103746); the Museo Nacional de Ciencias Naturales and the Ministerio del Ambiente, in Quito, for arranging the necessary permits for research in Ecuador; Keith Willmott (Fig. 2A,B) and Jim Mallet (via Don Harvey) (Fig. 2C) for allowing me to reproduce their slides; Dan Janzen for the pupal photograph in Fig. 6B; Don Harvey for preparing the majority of the genitalia dissections listed in Table 2, helping to develop characters 32 and 33, and giving me access to his invaluable collections of appendage slides and early stage material; and Don Harvey, Richard Vane-Wright and two anonymous reviewers for critical comments on the manuscript.

References

Bates, H.W. (1868) A catalogue of Erycinidae, a family of diurnal Lepidoptera. *Journal of the Linnean Society (London) (Zoology)*, **9**, 373–459.

Beutelspacher, C.R. (1972) Some observations on the Lepidoptera of bromeliads. *Journal of the Lepidopterists' Society*, **26**, 133–137.

Biezanko, C.M., Mielke, O.H.H. & Wedderhoff, A. (1979) Contribuição ao estudo faunístico dos Riodinidae do Rio Grande do Sul, Brasil (Lepidoptera). *Acta Biologica Paranaense*, **7**, 7–22.

Bremer, K. (1988) The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution*, **42**, 795–803.

Bremer, K. (1994) Branch support and tree stability. *Cladistics*, **1**, 295–304.

Brévignon, C. (1992) Elevage de deux Riodininae guyanais, *Napaea beltiana* Bates et *Cremna thasus* Stoll. 1. A propos de la myrmécophilie des chenilles (Lep. Lycaenidae Riodininae). *Alexanor*, **17**, 403–413.

Brévignon, C. (1993) Elevage de deux Riodininae guyanais, *Napaea beltiana* Bates et *Cremna thasus* Stoll. 2. La comportment des imagos (Lep. Lycaenidae Riodininae). *Alexanor*, **17**, 508–512.

Brévignon, C. & Gallard, J.-Y. (1997) Inventaire des Riodinidae de Guyane Française II – Riodininae: Mesosemiini, Eurybiini, incertae sedis. Description de nouveaux taxa. (Lepidoptera). *Lambillionea*, **97**, 322–342.

Brévignon, C. & Gallard, J.-Y. (1999) Inventaire des Riodinidae de Guyane Française VI – Riodininae: Nymphidiini, Stalachtini. Description de nouveaux taxa. Deuxième partie. (Lepidoptera). *Lambillionea*, **99**, 277–290.

Bullock, S.H. (1990) Host records for some tropical phytophagous and parasitic insects. *Pan-Pacific Entomologist*, **66**, 252–254.

Callaghan, C.J. (1993) Notes on the immature biology of two riodinine butterflies: *Metacharis ptolomaeus* and *Napaea nepos orpheus* (Lycaenidae). *Journal of Research on the Lepidoptera*, **30**, 221–224.

Clench, H.K. (1955) Revised classification of the butterfly family Lycaenidae and its allies. *Annals of the Carnegie Museum*, **33**, 261–274.

Comstock, J.H. & Needham, J.G. (1918) The wings of insects. *American Naturalist*, **32**, 231–257.

Cottrell, C.B. (1984) Aphytophagy in butterflies: its relationship to myrmecophily. *Zoological Journal of the Linnean Society*, **80**, 1–57.

DeVries, P.J. (1988) The larval ant-organs of *Thisbe irenea* (Lepidoptera: Riodinidae) and their effects upon attending ants. *Zoological Journal of the Linnean Society*, **94**, 379–393.

DeVries, P.J. (1997) *The Butterflies of Costa Rica and Their Natural History II: Riodinidae*. Princeton University Press, Princeton, New Jersey.

DeVries, P.J. & Baker, I. (1989) Butterfly exploitation of an ant-plant mutualism: adding insult to herbivory. *Journal of the New York Entomological Society*, **97**, 332–340.

DeVries, P.J., Chacón, I.A. & Murray, D. (1994) Toward a better understanding of host use and biodiversity in riodinid butterflies (Lepidoptera). *Journal of Research on the Lepidoptera*, **31**, 103–126.

DeVries, P.J. & Penz, C.M. (2000) Entomophagy, behavior, and elongated thoracic legs in the myrmecophilous Neotropical butterfly *Alesa amesis* (Riodinidae). *Biotropica*, **32**, 712–721.

Eliot, J.N. (1973) The higher classification of the Lycaenidae (Lepidoptera): a tentative arrangement. *Bulletin of the British Museum of Natural History (Entomology)*, **28**, 373–506.

Eriksson, T. (1998) *AUTODECAY, Version 4.0*. Department of Botany. Stockholm University, Stockholm, distributed by the author.Evans, W.H. (1949) *A Catalogue of the Hesperiidae from Europe, Asia and Australia in the British Museum (Natural History)*. British Museum (Natural History), London.

Farris, J.S. (1969) A successive approximations approach to character weighting. *Systematic Zoology*, **18**, 374–385.

Felsenstein, J.F. (1985) Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*, **39**, 783–791.

Guppy, P.J.L. Jr (1904) Notes on the habits and early stages of some Trinidad butterflies. *Transactions of the Entomological Society of London*, **1904**, 225–228.

Hall, J.P.W. (1998) A review of the genus *Sarota* (Lepidoptera: Riodinidae). *Tropical Lepidoptera*, **9** (Suppl. 1), 1–21.

Hall, J.P.W. (1999) *A Revision of the Genus* Theope. *Its Systematics and Biology (Lepidoptera: Riodinidae: Nymphidiini)*. Scientific Publishers, Gainesville, Florida.

Hall, J.P.W. (2002) Phylogeny of the riodinid butterfly subtribe Theopeina (Lepidoptera: Riodinidae: Nymphidiini). *Systematic Entomology*, **27**, 139–167.

Hall, J.P.W. & Harvey, D.J. (2001) A phylogenetic analysis of the Neotropical riodinid butterfly genera *Juditha*, *Lemonias*, *Thisbe* and *Uraneis*, with a revision of *Juditha* (Lepidoptera: Riodinidae: Nymphidiini). *Systematic Entomology*, **26**, 453–490.

Hall, J.P.W. & Harvey, D.J. (2002) A survey of androconial organs in the Riodinidae (Lepidoptera). *Zoological Journal of the Linnean Society*, **136**, 171–197.

Harvey, D.J. (1987) *The Higher Classification of the Riodinidae (Lepidoptera)*. PhD Dissertation. University of Texas, Austin, Texas.

Horvitz, C.C., Turnbull, C. & Harvey, D.J. (1987) Biology of immature *Eurybia elvina* (Lepidoptera: Riodinidae), a myrmecophilous metalmark butterfly. *Annals of the Entomological Society of America*, **80**, 513–519.

Janzen, D. & Hallwachs, W. (2002) Philosophy, navigation and use of a dynamic database ('ACG Caterpillars SRNP') for an inventory of the macrocaterpillar fauna, and its food plants and parasitoids, of the Area de Conservacion Guanacaste (ACG), northwestern Costa Rica. http://janzen.sas.upenn.edu.

Klots, A.B. (1956) Lepidoptera. *Taxonomists' Glossary of Genitalia in Insects* (ed. by S. L. Tuxen), pp. 97–110. Munksgaard, Copenhagen.

Maddison, W.P. & Maddison, D.R. (1995) *MacClade: Analysis of Phylogeny and Character Evolution, Version 3.05*. Sinauer Associates, Sunderland, Massachusetts.

Meerman, J.C. (1999) Lepidoptera of Belize. 1. Catalog of butterflies (Lepidoptera: Papilionoidea). *Tropical Lepidoptera*, **10**(Suppl. 1), 7–32.

Müller, J.F.T. (1877) Os órgãos odoriferos nas pernas de certos lepidópteros. *Archivos do Museu Nacional do Rio de Janeiro*, **2**, 37–46.

Reuter, E.F. (1896) Über die Palpen der Rhopalocera. Ein Beitrag zur Erkenntnis der verwandtschaftlichen Beziehungen unter den Tagfaltern. *Acta Societatia Scientiarum Fennicae*, **22**, 1–577.

Stehr, F.W. (1987) *Immature Insects*. Kendall-Hunt Publishing Co, Dubuque, Iowa.

Stichel, H.F.E.J. (1910–11) Family Riodinidae. Allgemeines. Subfamily Riodininae. *Genera Insectorum*, **112**, 1–452.

Stichel, H.F.E.J. (1928) Lepidoptera Nemeobiinae. *Das Tierreich*, **51**, 1–330.

Stichel, H.F.E.J. (1930–31) Riodinidae. *Lepidopterorum Catalogus, Vol. 38–41* (ed. by E. Strand), pp. 1–795. Dr W. Junk, Berlin.

Swofford, D.L. (1999) PAUP*: Phylogenetic Analysis Using Parsimony (*and Other Methods), Version 4.0b4a. Sinauer Associates, Sunderland, Massachusetts.

Zikán, J.F. (1920) Biologische Beiträge zur Schmetterlingsfauna Brasiliens. *Deutscher Verein für Wissenschaft und Kunst*, **1**, 145–157.

Zikán, J.F. (1953) Beiträge zur Biologie von 19 Riodiniden-Arten (Riodinidae – Lepidoptera). *Dusenia*, **4**, 403–413.

Accepted 5 March 2002

Appendix 1. Data matrix for the phylogenetic analysis. Missing data are represented by '?'.

Taxon					5					10					15					20					25					30					35
Euselasia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eunogyra	1	0	0	0	0	0	0	1	?	0	0	0	1	0	0	0	0	1	1	0	0	3	1	1	0	0	3	?	?	?	?	?	?	?	?
Teratophthalma	1	1	0	0	0	0	0	1	?	0	0	0	1	1	0	0	0	1	1	0	0	3	1	1	0	0	?	?	?	?	?	?	?	?	?
Mesosemia	1	1	0	0	0	0	0	1	?	0	0	0	1	1	1	0	0	0	1	0	0	2	1	1	1	0	2	0	1	1	1	0	0	0	1
Leucochimona	1	1	0	0	0	1	0	1	?	0	0	0	1	1	1	0	0	0	1	0	0	2	1	1	1	0	2	0	1	1	1	0	0	0	1
Semomesia	1	1	0	0	0	1	0	1	?	0	0	0	1	1	1	0	0	0	1	0	0	2	1	1	1	0	?	?	?	?	?	?	?	?	?
Perophthalma	1	1	0	0	0	1	0	1	?	0	1	0	1	0	1	0	0	0	1	0	0	2	1	1	1	0	2	0	1	1	1	0	0	0	1
Mesophthalma	1	1	0	0	0	1	0	1	?	0	1	0	1	1	1	0	0	0	1	0	0	2	1	1	1	0	?	?	?	?	?	?	?	?	?
Hyphilaria	1	0	0	1	0	0	0	1	?	0	0	0	1	0	0	0	0	1	1	1	0	4	1	0	0	1	4	0	?	0	1	?	?	1	0
Cremna	1	0	0	1	0	0	0	0	0	1	0	1	1	0	0	1	0	1	1	1	0	5	1	0	0	1	4	0	?	?	?	?	?	?	?
Napaea	1	0	0	1	0	0	0	1	?	1	0	0	1	0	0	1	0	1	1	1	0	5	1	0	0	1	4	0	1	1	1	0	0	1	0
Voltinia	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	5	1	0	0	1	?	?	?	?	?	?	?	?	?
Eucorna	?	0	?	0	0	0	0	1	?	0	0	1	1	0	0	0	0	1	1	1	0	5	1	0	0	1	?	?	?	?	?	?	?	?	?
Ithomiola	1	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	1	1	1	0	5	1	0	0	1	4	0	1	1	1	?	?	1	0
Hermathena	1	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	1	1	1	0	5	1	0	0	1	4	0	?	1	1	0	0	1	0
Alesa	2	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1	1	0	0	0	?	1	1	0	1	1	1	?	0
Eurybia	2	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1	1	0	0	0	1	1	1	0	1	1	1	0	0
Riodina	2	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	6	1	0	0	0	?	0	1	0	1	1	0	0	0
Esthemopsis	2	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	7	1	0	0	0	?	0	1	0	1	1	0	0	0

Appendix 2. List of species whose pupae have been examined for characters 32 and 33 in the phylogenetic analysis.

Nemeobiinae	
Nemeobiini	*Hamearis lucina* (Linnaeus)
Zemerini	*Zemeros flegyas* (Cramer)
	Dodona ouida Moore
Euselasiinae	*Euselasia mys* Herrich-Schäffer
	Euselasia midas (Fabricius)
	Hades hecamede Hewitson
Riodininae	
Mesosemiini	*Perophthalma lasus* Westwood
	Leucochimona lepida (G. & S.)
	Mesosemia cippus Hewitson
	Mesosemia telegone (Boisduval)
	Napaea eucharila (Bates)
	Hermathena nr *candidata* (Hewitson)
Eurybiini	*Eurybia lycisca* Westwood
	Eurybia elvina Stichel
	Alesa rothschildi (Seitz)
Riodinini	*Lyropteryx apollonia* Westwood
	Ancyluris aulestes (Cramer)
	Rhetus periander (Cramer)
	Chorinea amazon (Saunders)
	Riodina lysippoides Berg
	Riodina lycisca (Hewitson)
	Chalodeta theodora (C. & R. Felder)
Riodininae	
Symmachiini	*Esthemopsis pherephatte* (Godart)
Helicopini	*Helicopis cupido* (Linnaeus)
	Helicopis gnidus (Fabricius)
	Anteros bracteata Hewitson
	Anteros renaldus (Stoll)
incertae sedis (4FRV)	*Emesis mandana* (Cramer)
	Calydna sturnula (Geyer)
	Argyrogrammana crocea (G. & S.)
Stalachtini	*Stalachtis phlegia* (Cramer)
	Stalachtis lineata (G.-Méneville)
Nymphidiini	*Lemonias zygia* Hübner
	Thisbe irenea (Stoll)
	Synargis abaris (Cramer)
	Synargis orestessa Hübner
	Juditha caucana (Stichel)
	'*Calospila*' *cilissa* (Hewitson)
	'*Calospila*' *emylius* (Cramer)
	*Menander menande*r (Stoll)
	Nymphidium cachrus (Fabricius)
	Nymphidium mantus (Cramer)
	Nymphidium minuta H. Druce
	Theope virgilius (Fabricius)

[Note added in proof: I have now examined numerous eggs of Napaeina species collected from several species of orchids in eastern Equador. As these eggs all lack spines, I can now tentatively propose the presence of spines at the vertices of the hexagonal sculpturing on eggs as an additional synapomorphy for Mesosemiina.]